

Research Article

Does Experience Affect the Outcome of Male-Male Contests in the Burying Beetle, *Nicrophorus quadripunctatus*?

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The bigger individual in a fight usually wins unless the smaller individual is a resident or has recently won a fight. I conducted three experiments on the effects of body size, residency, and fight history on the outcome of male-male fights in a burying beetle. Fights were staged between an intruding male and the male of a male-female pair. When males differed in size, the larger male usually won regardless of residency or individual fight histories. Residents and winners of previous fights won only when competing males were similar in size. Hence, male body size largely determines the outcomes of fights in this beetle.

1. Introduction

Fighting between males over mating opportunities is a widespread phenomenon in the animal kingdom and has received much empirical attention [1]. Fighting ability is often correlated with morphological and physiological attributes such as body size, weaponry, and ornaments [1], but these are not the only attributes that may determine fighting ability. It has been hypothesized that the “prior residence effect” can also affect the outcome of fighting contests in accordance with the convention “resident wins, intruder retreats” [2]. A third effect is the “winner-loser effect,” in which winners are more likely to win again and losers are more likely to lose again [3]. These two effects sometimes counteract morphological and physiological attributes (e.g., [4]).

The complex parental behaviour of burying beetles (*Nicrophorus*: Silphidae) has been well-studied (reviewed in [5, 6]). *Nicrophorus* exploits small vertebrate carrions as food for its young. A male-female pair prepares a carcass by burying it, removing its hair, and rounding it into a ball. Eggs are then laid in the soil adjacent to the carrion ball. After hatching, the larvae crawl to the carrion ball, where they are fed by parental regurgitations. *Nicrophorus* is generally monogamous [7–9], and both sexes display intense intrasexual competition [10, 11]. Two or more individuals of both sexes often locate the same carcass, but usually only a single dominant pair eventually occupies the carcass.

Resident males are more likely to be injured than resident females [12], and males have a greater tendency to guard [13, 14]. Contests between males are expected to be more intense than those between females.

Larger individuals of *Nicrophorus* usually win contests among conspecifics in *N. humator* [10] or in *N. quadripunctatus* [11]. However, the presence of the winner effect is supported by a previous study of *N. humator* [15], and it is possible that other attributes affect the outcomes of such contests. In this study, I investigated whether the outcomes of male-male contests in *Nicrophorus quadripunctatus* differ in accordance with the prior residence effect and/or winner-loser effect.

2. Materials and Methods

All beetles were caught in the field in Nagaoka City, Niigata Prefecture, Japan using hanging traps baited with rotten meat. Injured individuals were excluded from the experiments. The beetles were maintained individually for more than 7 days so that they would lose the memories of past fighting. They were fed small pieces of chicken *ad libitum*. The pronotal width of each beetle was measured before the experiment. Medium-sized beetles (pronotal width 4.5–5.0 mm) were used to make pairs. A male and female pair was placed along with a small piece of chicken meat (approx. 15 g) in a plastic

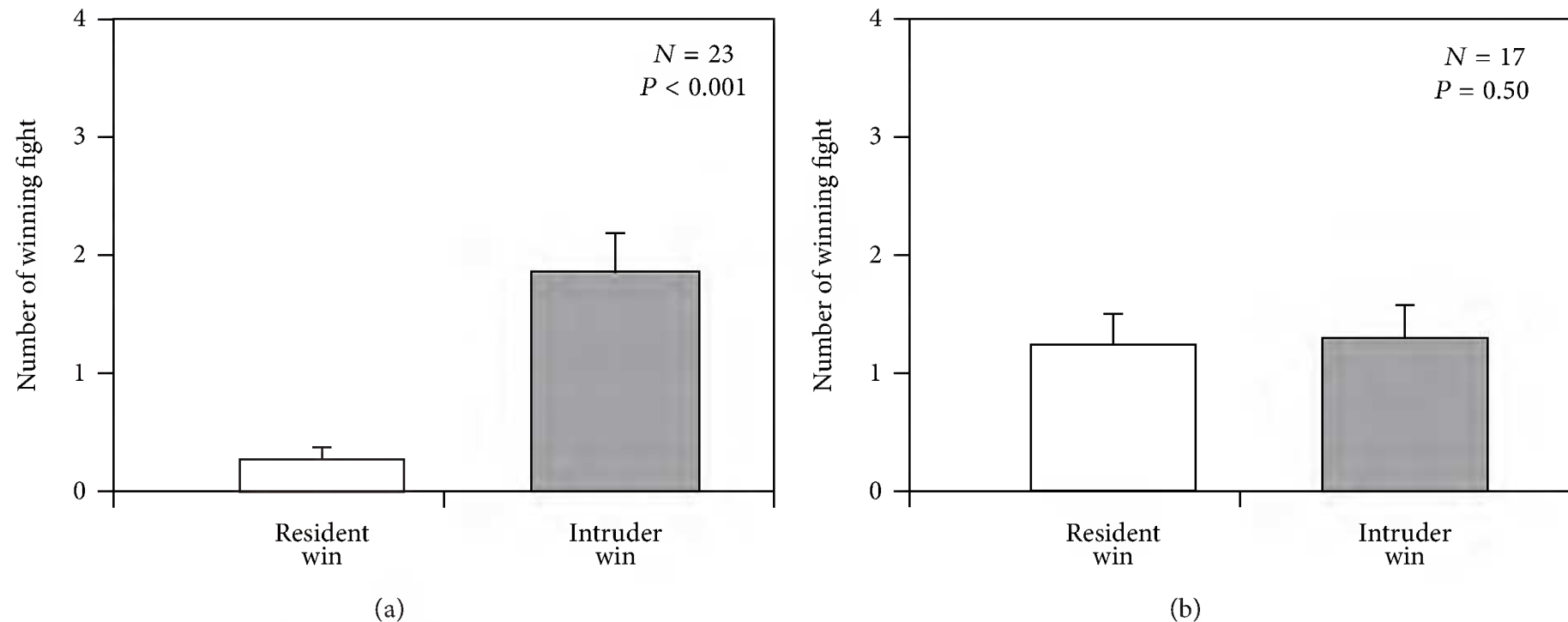


FIGURE 1: The times individuals took in winning fights in the control contest (experiment 1). (a) A larger intruder was introduced. (b) A similar-sized intruder was introduced. The data are means \pm standard error (SE).

arena (150 \times 150 \times 50 mm). The arenas were maintained under standard laboratory conditions of light and ambient temperature. Beetles for intruder males were sorted into large (pronotal width 5.5–6.5 mm) and same-sized males (pronotal width less than 0.2 mm different from that of the resident male).

Experiment 1 (control contest): the male/female pair remained in an arena for 1 h. A large male ($N = 23$) or a same-sized male ($N = 17$) was introduced as the intruder.

Experiment 2 (effect of residence): a beetle pair was maintained in an arena for 6 h. A large ($N = 20$) or same-sized male ($N = 22$) was introduced in the arena at 6 h as an intruder. Because many of the carcasses had been buried within 8 hours [16], I regarded 6 hours as enough time for pair formation.

Experiment 3 (effect of prior experience): a pair was maintained in an arena for 1 h. A larger or a smaller-size male (pronotal width difference more than 10% of the resident male) was introduced and observed until the first contest. The beetle that escaped the place first was regarded as the loser, and the beetle that stayed as the winner if body contact between males had occurred. All beetles that were placed with larger male had lost and all beetles that were placed with smaller male had won the first contest. After the fate of the contest between first introduced beetle was confirmed, the introduced male was removed and another new large male ($N = 16$), or same-sized male (winner: $N = 20$, loser: $N = 20$), was immediately introduced as an intruder. If the resident male injured its antenna or a leg in the first contest, it was excluded from the experiment.

After a male was introduced as an intruder, the behavioural interactions of all of the beetles were recorded for 1 h. When an aggressive interaction [11] occurred between the males, the number of contest and the fate of the contest were recorded. The beetle that escaped the place first was regarded as the loser, and the beetle that stayed was regarded as the winner if body contact between males had occurred. Because the contest was repeated during observation time,

the fate of all contests was recorded. The number of contests that residents or intruders won was regarded as the indicator of the fate of contests.

Generalized linear models (GLM) with binomial distributions were used to examine differences in the fate of contests between resident and intruder male. Significance was accepted at $P < 0.05$.

3. Results

Experiment 1 (control contest): when the intruder was larger than the resident male, the resident male usually lost the contest ($t = 7.32$, $P < 0.001$). In contrast, when the intruder was same-sized, about half of the residents lost the contest ($t = 0.42$, $P = 0.50$, Figure 1).

Experiment 2 (effect of resident): when the intruder was larger than the resident male, the resident usually lost the contest ($t = 5.21$, $P < 0.001$). In contrast, when the intruder was same-sized, most of the residents won the contest ($t = 4.08$, $P < 0.001$, Figure 2).

Experiment 3 (effect of prior experience): whether the resident males had winning or losing contest experiences, most of them lost to the next large intruder (Figure 3). When the intruder was same-sized, the residents that had had a winning experience usually won the contest ($t = 2.52$, $P = 0.008$, Figure 3). In contrast, most of the residents that had had a losing experience did not win these contests ($t = 1.29$, $P = 0.21$, Figure 3). In addition, fewer fights were started by the males that had had a losing experience compared to the males that had had a winning experience (t -test, $t = 2.04$, $P = 0.04$).

In all experiments, no intersexual contests were observed.

4. Discussion

In *Nicrophorus* spp., even after oviposition and hatching, infanticidal takeovers by intruding individuals occur regularly in the field [17]. Intruders kill the eggs and larvae of

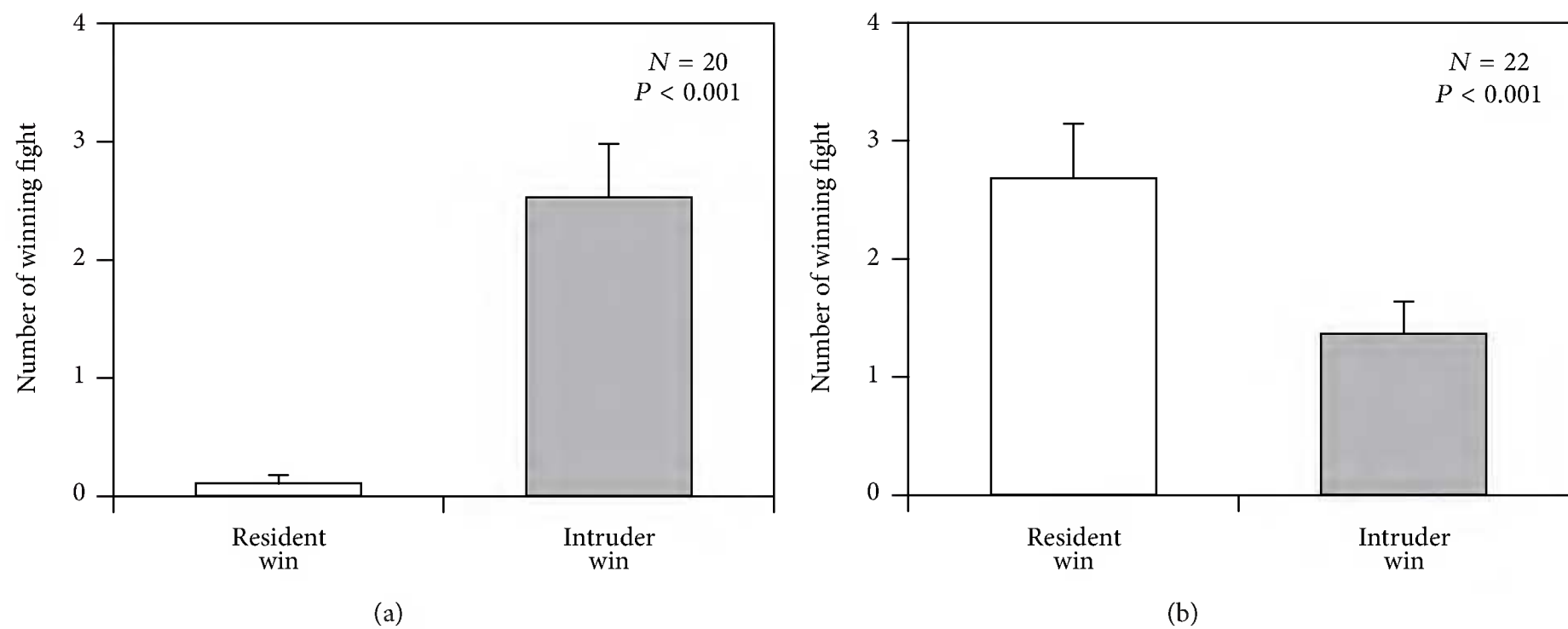


FIGURE 2: The times individuals took in winning fights in the prior experienced contest (experiment 2). (a) A larger intruder was introduced. (b) A similar-sized intruder was introduced. The data are means \pm SE.

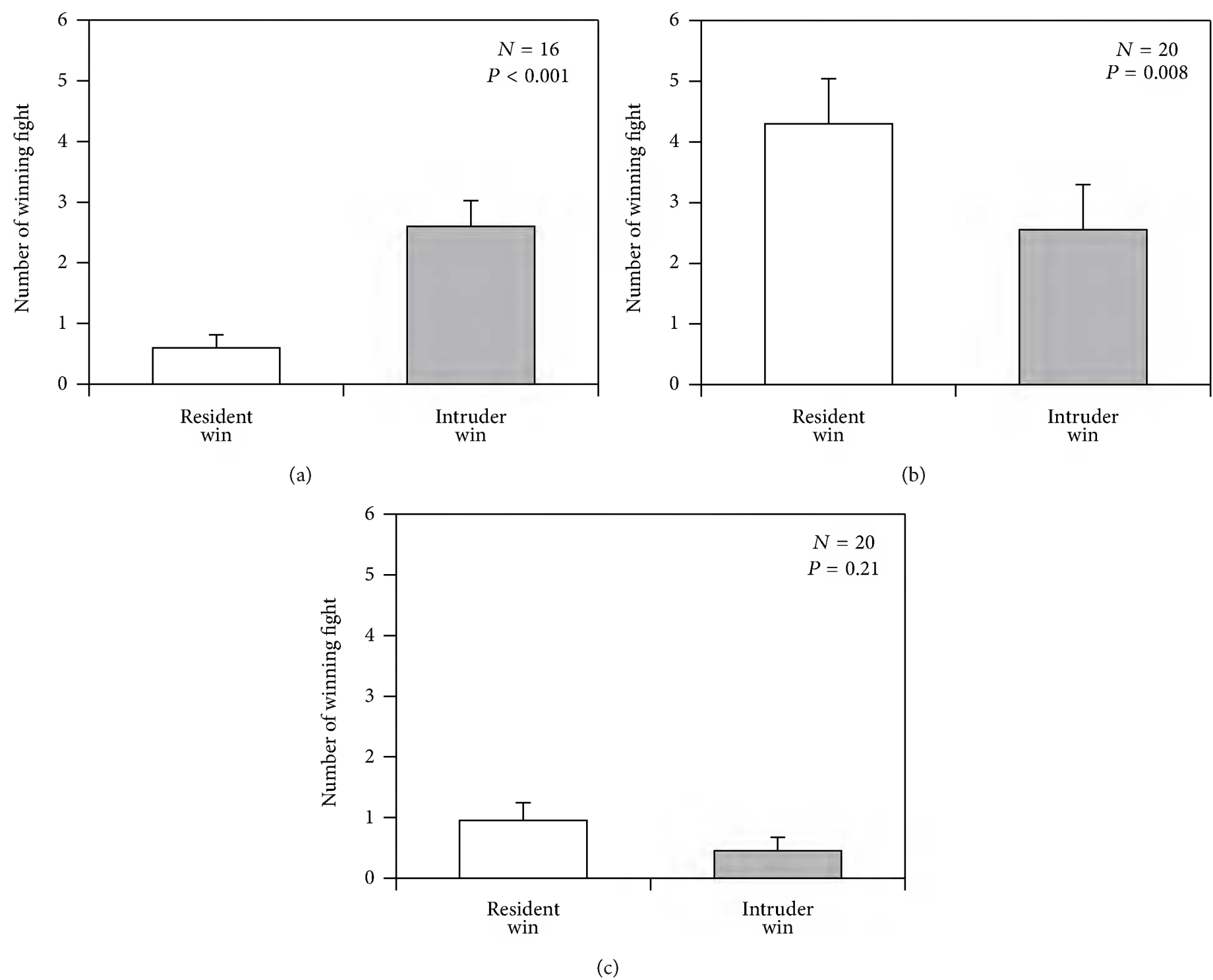


FIGURE 3: The times individuals took in winning fights in the winner-loser contest (experiment 3). (a) A larger intruder was introduced to the arena where the male had just had a winning experience. (b) A similar-sized intruder was introduced to the arena where the male had just had a winning experience. (c) A similar-sized intruder was introduced to the arena where the male had just had a losing experience. The data are means \pm SE.

the residents and reproduce on the carcass [18]. Since infanticide reduces the reproductive success of the resident parents, it is advantageous for both parents to reduce the possibility of infanticide. Many studies have shown that size is an important asymmetry in *Nicrophorus* competition [10, 11, 19]. Larger beetles have a better chance of possessing a carcass and of displacing a resident and taking over a buried carcass [12, 17]. The results of the present study also indicated that larger males are more likely to win a male-male contest. However, it has been reported that smaller *Nicrophorus* individuals can repel a larger intruder [20, 21]. Biparental cooperation can also affect the fate of contests; a male-female pair can usually repel a larger male intruder [20]. However, because most contests involve resident males and because repelling larger intruders occurs after the burial of carcasses [21], the possibility of the effect of male prior residence or other effects remains.

In the present study, when the body size of the intruder male was similar to that of the resident male, the effect of prior residence seems to be paramount, but the effect of prior residence did not override the difference in body size (Figure 2).

The experience of winning had an effect on the contests between same-sized males; however, the winner effect also did not override the difference in body size (Figure 3). It has been said that the loser effect often has more effect than the winner effect [22]. According to the self-assessment hypothesis, prior fighting experience could be used to assess one's own fighting ability relative to that of others in the population [23]. The present study's results showed that the males that had losing experiences had not only lower rates of winning but also fewer contests with same-sized males. When a burying beetle loses a fight, body damage is often incurred [21].

Because the fighting ability of burying beetles depends in part on their body size, a male that has already lost a fight may be reluctant to fight even a similar-sized intruder. Males that have had a losing experience may avoid fighting altogether. Males that have experience winning will defend resources more aggressively, and losing males will defend them less aggressively when the body size of the intruder is not larger.

Biparental cooperation can repel intruder beetles [20]. In the present experiments, no females attacked the intruder males, and thus, biparental cooperative defence did not occur. Intersexual contests in *N. quadripunctatus* before carrion burial have not been reported [11], and biparental cooperation is restricted after parental care begins [20]. Thus, the outcome of fights will be determined by the resource-holding power of resident males. Since the effect of prior residence seems not to override the difference of body size, the fate of male-male contests will be body size-dependent. Thus, if a male is challenged by a larger male before the completion of a carrion burial, they may lose the carcass.

The results of the present study suggest the presence of an effect of prior residence and the winner-loser effect in *Nicrophorus* males, but larger males still usually win the male-male contests. Only biparental cooperation has been reported to override body-size differences in male-male competitions among *Nicrophorus* burying beetles.

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